

First record of extra-abdominal processes in adult Odonata

Natalia A. Matushkina*

Department of Zoology, Institute of Biology, Taras Shevchenko National University of Kyiv, Kyiv, Ukraine

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Paired extra-abdominal processes (ap) were found in the pleural region of abdominal segments 6–9 in adult Odonata for the first time. They are unsegmented bulge-like or rod-like structures of different size, degree of sclerotization and movability. A short search across odonatan families has shown that ap are inherent for all studied Aeshnidae and for some other Anisoptera. A comparative study of final stadium larvae has shown that ap appear as remnants of larval lateral spines originally situated on larval tergites. This fact provides evidence about the complex nature of the pleural region in the Aeshnidae imago which includes part of the area of the larval tergite.

Keywords: comparative morphology; homology; appendages; abdomen; heterochrony; Odonata; dragonfly

Introduction

Abdominal appendage-like processes in insects have attracted special interest among scientists because they may help in understanding the early stages of insect evolution from an ancestor with developed abdominal legs (e.g. Bitsch, 2012; Suzuki & Palopoli, 2001). The homology-based theories of segment transformation in Arthropoda were often based on peculiar morphological characters, usually of presumed appendicular origin (e.g. Boxshall, 2004, 2013; Giorgianni & Patel, 2005; Kluge, 1989; Williams & Nagy, 2001). In immature insects, the abdominal appendages were structurally diverse and mostly appeared as simple integumentary outgrowths like prongs, spines or tubercles, located on the dorsal, lateral or ventral parts of the segments (see review by Bitsch, 2012). Some of these appendage-like processes, like abdominal gills in aquatic nymphs or prolegs of different endopterygote insect larvae, were regarded as derivatives of appendage anlagen (Bitsch, 2012; cf. Suzuki & Palopoli, 2001).

Although pterygote insects rarely exhibited the extra-abdominal appendages apart from the genitalia or cerci, most basal insect lineages (Archaeognatha and some Zygentoma) have a plesiomorphic richly structured abdominal venter bearing the styli and the coxal eversible vesicles, which were regarded as elements of appendicular origin (Bitsch & Bitsch, 2004; Klass & Matushkina, 2012). In adult Odonata, abdominal appendage-like structures not associated either with the genitalia or with the cerci have not previously been found.

Here I report paired abdominal processes (ap) found in the pleural region of abdominal segments 6–9 in adult Aeshnidae and some other Anisoptera, which has not previously been reported

*Email: odonataly@gmail.com

for Odonata. These structures were observed incidentally to a broad comparative morphological investigation of the female postabdomen in Aeshnidae (Odonata, Anisoptera); those observations led to the focus of this paper. I discuss the origin of ap in a framework of the segment homologization basing on the transformation of abdominal segments during metamorphosis.

Material and methods

Thirty-two adult females of 24 species of Odonata were investigated, including six specimens of three species of Zygoptera, one specimen of Epiophlebiidae, and 25 specimens of 20 species of Anisoptera (Table 1). Aeshnidae were chosen as a focus-group of this research for the reasons mentioned in the Introduction. Representatives of other dragonfly families, two fully developed final larvae of *Anax imperator*, and one fully developed larva of *Aeshna cyanea* were studied to test some hypotheses of developmental origin of ap.

All materials were first examined with a light microscope and then with a scanning electron microscope. For light microscopy, the abdomens were dissected dorsolaterally, soaked with c.10% water solution of lactic acid for 6–12 h to soften the cuticle (for dried specimens only), washed in water and macerated for 10–12 h at room temperature with 10% KOH. The macerated abdomens were thoroughly washed in distilled water and examined under glycerin with a stereo-microscope (Leica M205 C, Leica Microsystems, Museum of Zoology, Natural History Senckenberg Collections Dresden, Germany). For scanning electron microscopy, the cuticle parts were washed in distilled water, dehydrated in a graded ethanol series and acetone, and dried at the critical point (OM CPD 7501). Then cuticle parts were mounted on a stub, sputtered with gold-palladium (OM-SC7640) and examined with a Zeiss EVO-50 SEM (Zeiss, Museum of Zoology, Natural History Senckenberg Collections Dresden, Germany).

The terminologies of Klass (2008) and Matushkina (2008) were used for the abdominal skeleton of the dragonflies.

Results

Description of extra-abdominal processes

The abdominal segment of adult Odonata is characterized by an enlarged tergal region that forms dorsal, lateral and part of the ventral segment wall and by a narrowed sternal region that is partly covered by the tergum laterally. The membranous pleural region is invaginated into the body and can be partially exposed during respiration movements. The anterior half of the pleural region shows the spiracle in all abdominal segments anterior to the ninth segment. Sternal sclerotization bears bilateral cuticular ingrowths, the apodeme b (b7 in Figure 1), which is an attachment point for the dorsoventral muscle (muscle 15 in Klass, 2008; muscle dvp in Matushkina, 2008).

In pregenital segments ap is situated in the posterior half of the pleural region, behind the spiracle, equally far from the sternal and tergal sclerotizations. About at the level of ap the sternal sclerotization usually exhibits the apodeme b flanked by the dorsoventral muscles. Depending on the species, the position of ap in relation to the apodeme varies to some degree (Figure 1). Ventral regions of the eighth and ninth genital segments are modified due to location of genitalia. Sternal sclerotization of the eighth segment is shorter and wider as compared with the preceding segments; the basis of ap 8 is situated closer to the posterior edge of the segment. In ninth segments, the ventral region is entirely occupied by the ovipositor structures; ap 9 is situated very close to the posteroventral corner of the ninth tergite, on the inner membranous folding of the tergite. As a rule, ap are covered by surrounding cuticle and are not visible externally.

Table 1. Material examined in this study, presence of extra-abdominal appendage-like processes (ap) in adults and lateral spines in larvae.

Systematic assignment	Species	Number and kind of preservation	Presence of ap on 6/7/8/9 segment	Presence of sharp lateral spines in larva on 6/7/8/9 segment *
An.: Ae: Aeshnini	<i>Aeshna affinis</i> Vander Linden, 1820	1 et f	+ / + / + / + (conical)	± / + / + / +
An.: Ae: Aeshnini	<i>Aeshna cyanea</i> (Müller, 1764)	1 et f, 1 et l	+ / + / + / + (conical)	± / + / + / +
An.: Ae: Aeshnini	<i>Amphiaeschna ampla</i> (Rambur, 1842)	1 d f	- / + / + / - (conical)	?
An.: Ae: Aeshnini	<i>Coryphaeschna adnexa</i> (Hagen, 1861)	1 d f	- / + / + / - (vestigial)	- / ± / ± / ± (very slender)
An.: Ae: Aeshnini	<i>Rhionaeschna absoluta</i> (Calvert, 1952)	1 d f	- / + / + / + (vestigial)	?
An.: Ae: Anactini	<i>Anax imperator</i> Leach, 1815	4 et f, 2 et l	+ / + / + / +	+ / + / + / +
An.: Ae: Brachytronini	<i>Austroaeschna unicornis</i> (Martin, 1901)	1 d f	- / ± / ± / -	+ / + / + / +
An.: Ae: Brachytronini	<i>Brachytron pratense</i> (Müller, 1764)	1 et f	± / ± / ± / +	± / + / + / +
An.: Ae: Brachytronini	<i>Epiaeschna heros</i> (Fabricius, 1798)	2 d f	? / ± / ± / ±	+ / + / + / +
An.: Ae: Gomphaeschnini	<i>Basiaeschna janata</i> (Say, 1840)	1 d f	+ / + / + / - (well developed)	+ / + / + / + (all strong)
An.: Ae: Gomphaeschnini	<i>Boyeria vinosa</i> (Say, 1840)	2 d f	± / ± / ± / - (conical)	+ / + / + / + (all strong)
An.: Ae: Gomphaeschnini	<i>Gomphaeschna antilope</i> (Hagen, 1874)	1 d f	- / - / + / -	+ / + / + / +
An.: Ae: Gomphaeschnini	<i>Telephlebia tillyardi</i> Campion in Tillyard, 1916	1 d f	- / - / - / -	± / + / + / +
An.: Ae: Gynacanthagini	<i>Gynacantha adela</i> Martin, 1909	1 d f	- / ± / ± / -	+ / + / + / +
An.: Ae: Gynacanthagini	<i>Triacanthagyna septima</i> (Selys in Sagra, 1857)	1 d f	- / - / ± / -	?
An.: Petaluridae	<i>Phenes raptor</i> Rambur, 1842	1 d f	- / - / - / -	- / - / - / -
An.: Cordulegasteridae	<i>Cordulegaster bidentata</i> Selys, 1843	1 et f	- / - / - / -	- / - / - / -
An.: Corduliidae	<i>Epithea bimaculata</i> (Charpentier, 1825)	1 et f	- / - / + / +	- / - / + / +
An.: Gomphidae	<i>Gomphus vulgatissimus</i> (Linnaeus, 1758)	1 et f	- / - / - / -	- / - / - / -
An.: Libellulidae	<i>Orthetrum cancellatum</i> Linnaeus, 1758	1 et f	- / - / ± / ±	- / - / ± / ±
Az.: Epiophlebiidae	<i>Epiophlebia superstes</i> (Selys, 1889)	1 et f	- / - / - / -	- / - / - / -
Zyg.: Eupheidae	<i>Epallage fatime</i> (Charpentier, 1840)	2 et f	[+ / + / + / -] (vestiges)	[+ / + / + / -] (gills)
Zyg.: Calopterygidae	<i>Hetaerina americana</i> (Fabricius, 1798)	3 et f	- / - / - / -	- / - / - / +
Zyg.: Coenagrionidae	<i>Coenagrion pulchellum</i> (Vander Linden, 1825)	1 et f	- / - / - / -	- / - / - / -

*Based on literature data and unpublished observations. Abbreviations: et, in ethanol; d, dry; f, female; l, final larva; An., Anisoptera; Ae., Aeshnidae; Az., Anisozygoptera; Zyg., Zygoptera; +, large; ±, medium; -, small or absent; [...], presence of larval gills and their vestiges; ?, information absent.

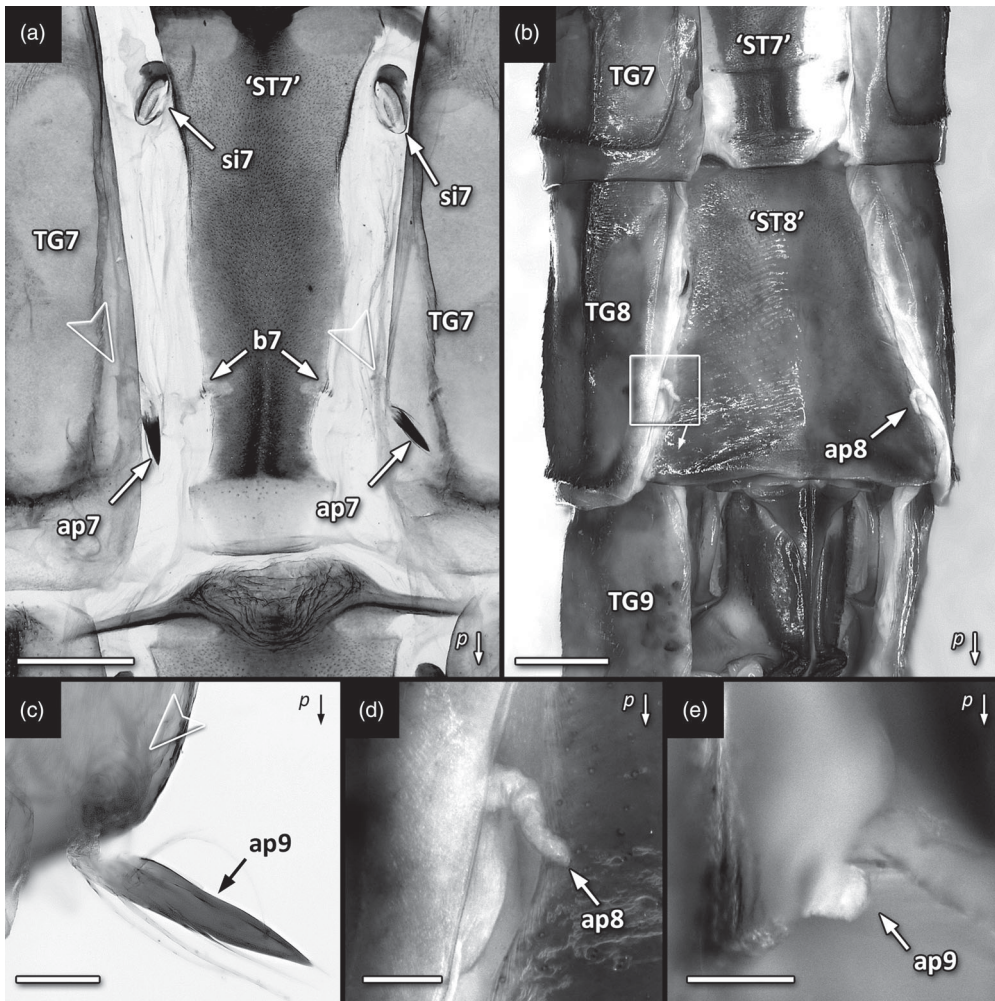


Figure 1. Variety of appendage-like processes in females of *Anax imperator*, light microscopy: (a) macerated seventh segment ventrally; (b) non-macerated eighth segment ventrally with inset enlarged in (d); (c–e) morphological variability of appendage-like processes. ap7, ap8, ap9, processes on pleural area of seventh, eighth and ninth segment wall, respectively; b7, postspiracular apodeme on seventh sternum; p, posterior direction; si7, spiracle of seventh segment; “ST7”, “ST8”, seventh and eighth sternums, respectively (for sclerite composition of sternum in dragonflies see Klass 2008); TG7, TG8, TG9, seventh, eighth and ninth tergites, respectively. Empty arrowhead indicates proximal end of process ap. Scale bars: (a), (b) 0.001 mm; (c–e) 0.2 mm.

Each ap is a hollow unsegmented outgrowth of the body wall without intrinsic muscles or tracheation. One newly emerged specimen of *Anax imperator* was found to bear the most prominent ap (up to 1 mm long), which can be easily visible externally. Each ap consists of a narrow neck-like stalk with delicate membranous wall extending to a stiff sclerotized and melanized sharply pointed rod (Figures 1a, c, 2c, e). Similarly structured ap were found on the ninth segment in *A. parthenope*. Presence of the stalk implies these ap might be highly movable. Other teneral specimens of *Anax imperator* bear a weakly sclerotized worm-like ap 8 of c.350–400 mkm long (Figure 1b, d). Most usually, ap is represented by a weakly sclerotized conical outgrowth without evident waist (Figure 2b). The base of ap sclerotization may have a complex shape without clear margins, whereas the tip of ap is usually curved posteriorly. In *Epiaeschna heros*, a short ap8

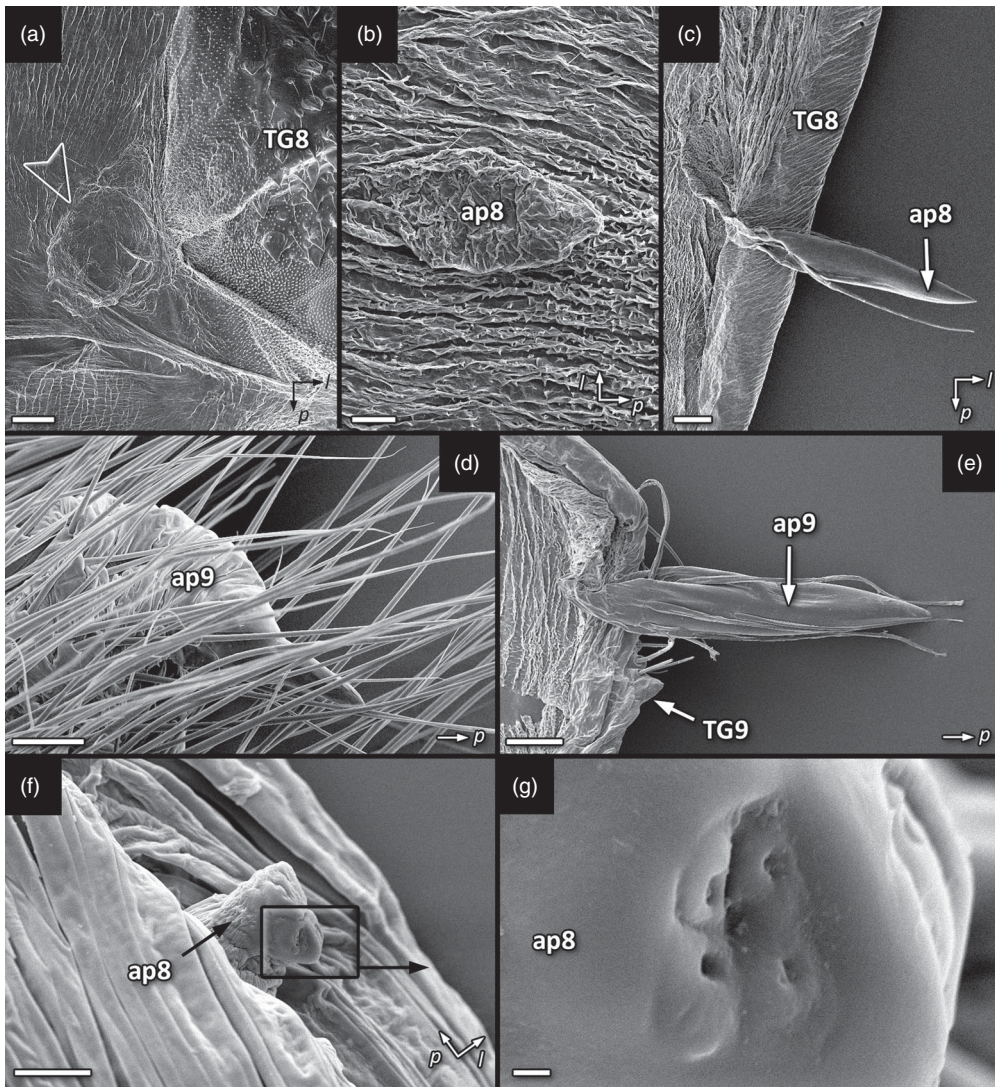


Figure 2. Comparison of vestigial larval gill by scanning electron microscopy in (a) female *Epallage fatima* (Euphaeidae); and (b–g) appendage-like processes in females of Aeshnidae: (b) *Aeshna affinis*; (c, e) *Anax imperator*; (d) *Brachytron pratense*; (f, g) *Epiaeschna heros*. TG8, TG9, eighth and ninth tergites, respectively; ap8, ap9, processes on pleural area of eighth and ninth segment wall, respectively. Empty arrowhead indicates vestige of larval gill. Double arrow indicates lateral (l) and posterior (p) directions. Scale bars: (a), (c), (e) 0.1 mm; (b) 0.3 mm; (d) 0.05 mm; (f) 0.02 mm; (g) 0.001 mm.

shows a regular apical sculpture (Figure 2f, g). Several specimens bear a very small membranous ap in the form of a nipple-shaped or finger-shaped protuberance or a bulge (Figure 1e). In case of its maximal reduction, ap appears as a swollen region of pleural membrane.

Fully developed or vestigial ap were found in all representatives of Aeshnidae on seventh–ninth abdominal segments (less often on seventh and eighth segments or on sixth–ninth segments) (see Table 1). In *Basiaeschna janata* ap were detected on fifth–eighth abdominal segments. Among other Odonata studied here, ap was found in *Epithecina bimaculata* (Corduliidae) and *Orthetrum cancellatum* (Libellulidae). Age of imago, its body size and degree of

sclerotization, taxonomic affiliation of the specimen and position on the abdomen apparently do not affect the morphology of ap.

Correspondence with larval lateral spines

Aeshnid larvae are characterized by prominent lateral spines on the posterior half of the abdomen (Table 1). These spines are very large, sharply pointed outgrowths of the lateral edge of 5–9 tergites which are gradually enlarged in subsequent segments. The region bearing the spine is not separated from the remaining tergite wall. The pleural region in a final instar larva consists of two well sclerotized plates – the triangular anterolateral one, PLa, and the posterior one, PLp (Figure 3a, d). Unlike in preceding segments, PLa 8 is very small and PLp 8 shows a clear transverse row of denticles that laterally ends at the lateral spine. PLp bears the remnant of the spiracle “si” as a dark well-bordered patch situated in its anterior region. In the studied final larvae with developed imaginal cuticle under the larval cuticle, the larval spine represents a mostly empty outgrowth bearing only a small soft, pale ap inside (Figure 3a–c). In the imago, instead of the firm larval pleural plates there is a mostly membranous area (Figure 3d, e). Thus, the membrane situated between the tergite TG and sternite ST of an abdominal segment bears in the imago two evident structures – the spiracle si and the abdominal process ap (Figure 3e).

Comparison with vestiges of larval gills

Euphaeidae and Polythoridae are only recent Odonata with supplementary larval gills running down the sides of the abdomen (Lok & Orr, 2009). In *Epallage fatime* (Zygoptera, Euphaeidae), the gill is a movable grub-like hollow appendage with intrinsic tracheation and one muscle connecting the gill base with the respective tergite; thus the gills are movable and functionally loaded appendages. The gills are attached to the pleural region of abdominal segments 2–8 bilaterally, just below the tergite and behind the spiracle vestige (Kluge, 2000). My investigation of adult *Epallage* shown that gills disappear to a small vestige in the form of a membranous convexity at the ventroposterior edge of tergites 2–8 (Figure 2a). If compared with the gill vestiges in *Epallage*, examined ap are as a rule more developed structures, which bear hairs, sclerotizations, and, as a rule, exhibit a definite shape. Topographically, ap and gill vestiges in *Epallage* are similar.

Discussion

Paired extra-abdominal processes (ap) are found in the pleural region of the sixth to ninth (rarely fifth to ninth) abdominal segments in several adult Anisoptera species. My study of final instar larvae show that the imaginal ap are developing under the cuticle of larval lateral spines, which occupy the posterolateral areas of the larval tergite. This fact leads to the assertion that the pleural region in adult abdominal segments of examined Odonata species corresponds topographically to the larval pleurite and to a part of the larval tergite. Consequently, the imaginal pleural region in the abdomen of Aeshnidae is of a complex pleuro-tergal origin (cf. Matushkina, 2008).

Why ap are appearing in adult Anisoptera, and whether they are of any functional importance, is an obscure matter. Larval aeshnid dragonflies are aquatic predators. Experiments provide evidence that spines of an anisopteran larva may serve as a defence tool against predators like fishes (Johansson & Samuelson, 1994; Mikolajewski & Johansson, 2004). However, spines might also be adaptations to other factors, such as keeping the larvae from sinking into the bottom substrate (Corbet, 1957) or helping them to cling to vegetation (Aguir, 1989). In Odonata, metamorphosis leads to drastic morphological modifications associated with the habitat shift from aquatic larvae

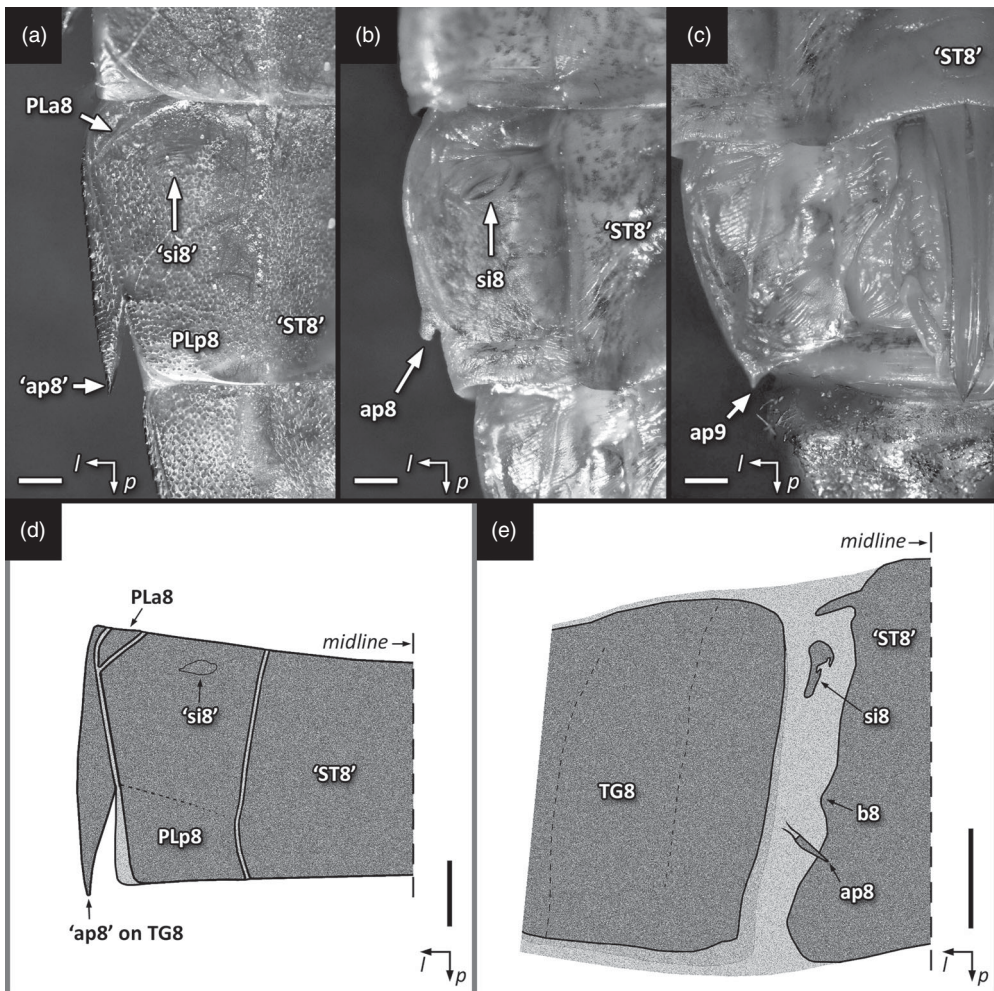


Figure 3. Ventral aspects of the eighth and ninth abdominal segment in Aeshnidae, right half shown only, (a–c) light microscopy, (d–e) diagrammatically. (a) The eighth abdominal segment of final larva of *Aeshna cyanea* and its imaginal cuticle underlying the larval cuticle (b); (c) imaginal cuticle underlying the larval cuticle of the ninth abdominal segment of final larva of *Aeshna cyanea*; (d), (e) ventral aspects of the eighth segment in final larva (d) and female (e) of *Anax imperator*. Segment wall in (e) is quasi bent ventrally and straightened. ap8, “ap8”, appendage-like process and lateral spine on tergite to which it is assumedly homologous, respectively; b8, postspiracular apodeme of eighth segment; PLa8, PLp8, anterior and posterior parts of pleurite, respectively; “ST8”, sternal sclerotization (for arguments for its complex origin see Klass 2008); si8, “si8”, spiracle sclerotization and its anlage on larval pleurite, respectively; TG8, eighth tergite. Grey scales in (d) and (e) indicate different degree of sclerotization. Double arrow indicates lateral (l) and posterior (p) directions. Scale bars: (a–c) 0.5 mm; (d) and (e) 0.001 mm.

to aerial adults (e.g. Leipelt, Suhling, & Gorb, 2010). Specifically in Aeshnidae, the abdomen becomes longer and slender, its tergites are enlarged and swollen and sternites are narrowed (Asahina, 1954). Whedon (1929) asserts that change of the shape of the abdomen in Odonata is apparently caused by change of respiration and locomotion mode. In aeshnid larvae, the abdomen ventilation movements consist of a rhythmic raising and lowering of the posterior abdominal venters (which include the sternite and pleural regions) against the terga; wherein the whole pleural region remains exposed during the ventilation cycle (Mill & Pickard, 1972). In contrast, the ventilation movements in the adult abdomen consist of alternate pulling of the narrow sternite deep inside the swollen tergite and subsequent protrusion of the sternite to its starting position; the

whole pleural region, including the area of ap, remains mostly hidden within the segment all the time. Therefore, ap remains deep in a slit between the abdominal tergite and sternite. This position makes unlikely any suggestion either on the exteroceptive or defence function of ap.

On the basis of the available data, I am inclined to consider that the ap are rather vestiges of firm larval spines that are retained in an imago. Indeed, the body of the freshly emerged imago in Odonata has several non-functional larval traits, especially in the musculature (Matushkina, 2008; Whedon, 1929), which may persist in the mature imago. However, virtually no information has previously been available on the changes undergone by peculiar outgrowths of the larval body wall, like prongs or spurs, in the metamorphosis to an imago. Further evidence in favour of residual non-functional origin of ap is lack of any traces of innervation and musculature associated with ap, and essential variability of the shape and degree of sclerotization of ap among specimens of the same species. A peculiarly structured apical surface of ap recorded from *Epiaeschna heros* remains obscure.

If my speculation about the non-functional origin of the found processes is true, it is unclear why Aeshnidae exhibit much more developed vestiges of larval spines (ap) as compared to the other dragonfly lineages studied, and as compared to diminutive vestiges of the larval gills in Euphaeidae. Perhaps the size and degree of sclerotization may affect the disappearance of cuticular structures during metamorphosis in some specific way. If so, very large dragonflies such as Aeshnidae have a better chance to retain firm, well-sclerotized larval cuticular structures in the imago. These issues require further investigation in order to deepen our fundamental knowledge about the insect body modification in the metamorphosis and the mechanism of the heterochronic development in the insects.

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